

# **Developmental pathway, speciation and supraspecific taxonomy in amphibians**

## **2. Developmental pathway, hybridizability and generic taxonomy**

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Several distinct developmental pathways exist in amphibians: free tadpoles feeding on external resources, tadpoles or embryos feeding on secretions from the mother or father, on their brothers or sisters, or on the internal vitelline reserves of the egg. A new terminology is proposed for these categories. It is suggested that generic taxonomy should take into account these developmental pathways, i.e. that species with free feeding tadpoles and species with other developmental modes should not be classified in the same genus or subgenus. Artificial hybridization between cladistically closely related species having different developmental pathways could provide interesting information both regarding evolutionary phenomena and supraspecific taxonomy. Detailed proposals are offered concerning how developmental pathways and hybridization data, combined with cladistic information on relationships, can be used in the generic taxonomy of amphibians. A new term is proposed for the concept of "relational taxonomic criterion" as defined by DUBOIS (1988).

### INTRODUCTION

In frogs, recent data on unusually high numbers of species of the direct-developing genus *Philautus* in Sri Lanka and southern India, as well as of species of the direct-developing genus *Eleutherodactylus* in central and southern America, led to the suggestion that such frogs are submitted during their development to "familial", rather than "individual", mortality, which could facilitate allele fixation in isolated populations and thus entail a speciation pattern different from that of other frogs (DUBOIS, 2004b). A suggested way of testing this hypothesis is through using metataxonomic data, e.g. the mean number of species per genus. Among the problems risen by this approach, however, is the fact that no unified "genus concept" is used by batrachologists and that genera recognized in different groups are not equivalent by any

standard. This problem of the equivalence of genera in different groups was already discussed at length elsewhere (DUBOIS, 1988), but these new elements lead me to come back to it under a new light.

The purpose of taxonomy is not to please taxonomists and phylogeneticists, but to provide useful information to other biologists and non-biologists, including environmental biologists, conservationists, ethologists, physiologists, etc. Among taxonomic categories, the genus plays a particularly rôle in this respect, as the generic nomen is included in the nomen of all species recognized by taxonomists and used for their works by other biologists (DUBOIS, 1988). If amphibian species do indeed show different patterns of speciation according to their developmental modes, inclusion of information on the developmental pathway would appear to be a crucial information to consider when recognizing genera. Among other things, this inclusion would facilitate the testing of this hypothesis, which is made difficult for the time being due to the fact that amphibian species bearing the same generic nomen may follow different developmental pathways.

Before going further, let us briefly explore the diversity of developmental pathways in amphibians.

#### CATEGORIES OF DEVELOPMENTAL PATHWAYS IN AMPHIBIANS

Developmental modes are indeed very varied in amphibians, especially in anurans. In some cases, all the pre-imaginal development<sup>1</sup> takes place away from the adult, within the egg, laid in a terrestrial or arboreal shelter: the embryo then depends only on the vitellus of the eggs for its resources. In other cases, the eggs are retained on the skin of the back or in a pouch of the parent of one sex (dorsal pouch, stomach, oviduct) but does not receive any feeding from the adult, thus depending also fully on the original vitelline reserves of the egg. Finally, in a few other cases, the embryo receives some feeding either directly from the adult or through eating some of the other embryos sharing its shelter within the mother's oviduct.

In the traditional usage of the terms "exotrophy" and "endotrophy" (e.g., THIBAUDIEAU & ALTIG, 1999) it is not clear what is considered "outside" and "inside" (designated by the roots *exo-* and *endo-*), if exotrophy is understood as "feeding from a resource external to the embryo or larva", then "endotrophy" should designate the opposite situation, i.e., "feeding from a resource internal to the embryo or larva", not "internal to the mother or father". Strictly speaking, in developmental terms the cases of feeding from resources provided by a parent or from brothers and sisters do not belong in the category of endotrophy but are in fact special cases of exotrophy that should better be designated under specific terms. Using a single category of endotrophy for such a variety of cases unites artificially several non-homologous modes of development derived independently from the tadpole model. As long as all the observed situations are not placed in a phylogenetic perspective, comparisons and reviews of these phenomena based on similarities and analogies (e.g.: LAMOTTE & LESCURE, 1977; WAKE, 1993; THIBAUDIEAU & ALTIG, 1999) but not on homologies will be of limited evolutionary interest. A better understanding of the evolution of these phenomena will require the

<sup>1</sup> Development between hatching and metamorphosis (in species with feeding larvae or embryos), or before hatching (in species in which the embryo relies only upon the egg's vitelline reserves for its development) (see table 1), which results in an *imagis* miniature copy of the adult but sexually immature (see DUBOIS, 1978: 2004ff).

obtention of robust cladistic hypotheses for the groups where these special developments occur, and detailed genetic, biochemical, physiological, ethological and ecological studies of the species concerned, as generalisation of the observations made on a few species may be misleading. Another important aspect of such approaches is to have a clear and unambiguous terminology to designate the various situations encountered in these groups.

Two aspects in particular must be distinguished in this respect, the *place* of the development of the embryo or larva (in the external environment, or within or upon one of the parents), and the origin of the *nutritional resources* used by this embryo or larva to reach the stage imago (in the external environment, or provided by one of the parents or by brothers and sisters). The place of development is interesting from an eco-ethological and evolutionary point of view, but by itself it does not provide relevant categories for the comparison of developmental pathways. For such comparisons, origin of nutritional resources is more important as it has direct consequences on the ontogenetic trajectory. Free larvae or embryos feeding on external resources, even within a pouch, differ from embryos maintained inside the egg capsule in several respects, regarding breathing, locomotion or feeding: thus they require precocious development of a functional digestive tract, earlier than in embryos feeding on vitelline resources, etc. Given the importance of trophic resources in developmental pathways, for more clarity I propose to use WOURMS's (1981) terminology and to expand it, as follows.

First of all, I propose to abandon the unclear terms "exotrophy" and "endotrophy" and to replace them, respectively, by *ergotrophy* (from the Greek *ergon*, "work") for species with free larvae that have to find their food in the external environment, and *argiotrophy* (from the Greek *argia*, "idleness, inaction") for species whose embryos are provided with food "passively" or almost so, either from their own vitellus or from the parents, brothers or sisters (DUBOIS, 2004b). Within the latter category, several subcategories can be distinguished.

The term *lecithotrophy* (from the Greek *lecithos*, "vitellus") is adequate to designate pre-imaginal development using only the vitelline reserves of the egg, without external feeding (WOURMS, 1981). Within this subcategory, two infracategories may be recognized: *leipolectitotrophy* (from the Greek *leipo*, "I abandon"), in which the eggs are "abandoned" by the parents and develop in an external shelter, and *stegolecithotrophy* (from the Greek *stegos*, "roof, house"), in which the eggs are either retained in the female genital tract after internal fertilization, or kept either upon or within one of the parents, after external fertilization.

The term *matrotrophy* (from the Greek *mater*, "mother") describes development using a secretion from the mother as nutritional resource (WOURMS, 1981). In frogs this is observed in the two known species of the bufonid genus *Nymbaphrynoides* (see e.g. : LAMOTTE & LESCURI, 1977; WAKL, 1993; THIBAUDAL & ALTIG, 1999). A parallel situation, not considered by WOURMS (1981) as it apparently does not exist in fishes, is *patrotrophy* (from the Greek *pater*, "father") for nutrition by a secretion from the father. In frogs, this seems to occur in *Rhmoderma darwini*, in which the embryos develop in the male vocal sac and receive feeding from the father, according to ГОРЮХИНА et al (1986). Matrotrophy and patrotrophy are infracategories of argiotrophy that can be grouped in a more general subcategory of *gonetrotrophy* (from the Greek *gonis*, "parents"), i.e. nutrition from a secretion by the parents.

In order to have a set of similarly formed terms, I propose to rename *adelphotrophy* (from the Greek *adelphos*, "brother") the subcategory recognized by WOURMS (1981) and many others as *adelphophagy*, for feeding on brothers and sisters inside the mother's oviduct. According to whether the brothers and sisters are eaten as eggs or as embryos, WOURMS (1981) distinguished *oophagy* from *adelphophagy*, which does not seem an important distinction as in both cases the origin of this nutritional resource is an egg inside the mother's oviduct. In contrast, he considered *oophagy* and *adelphophagy* as a subdivision of *matrotrophy*, which does not recognize the fact that in *matrotrophy* a *specific* secretion is produced by the mother to feed its embryos. It is exact that eggs and embryos eaten in *adelphotrophy* were also produced by the mother, but the vitellus of the egg also, so that if *adelphotrophy* was to be considered a subdivision of *matrotrophy*, this should also be the case for *lecithotrophy*.

Among all these developmental categories, as far as feeding of the embryo is concerned, *gonetrophy* and *adelphotrophy* are just special cases of "exotrophy", not of "endotrophy". The general ecological and developmental category *argiotrophy*, including *lecithotrophy*, *gonetrophy* and *adelphotrophy*, groups all species that are independent from feeding in the external environment during their development (DUBOIS, 2004b).

Finally, the fact that in some taxa the embryos are kept within a pouch in one of the parents is distinct from their nutritional resources. This can be accounted for by use of a general category of *gonephory* (from the Greek *phoros*, "bearing, carrying"), including *matrophory* and *patrophory* according to which parent is involved, but these are ecological categories, not categories of developmental pathways.

Table 1 summarizes the major features of each of the latter categories here defined, with examples in amphibians.

## DEVELOPMENTAL PATHWAYS AND GENERIC TAXONOMY

In frogs, it is striking to note that, among 325 anuran genera containing species whose development has, at least superficially, been described (see table 3 in DUBOIS, 2004b), 320 (i.e. 98.5%) are homogeneous with respect to their known main ecological and developmental category, i.e. either *ergotrophy* with free tadpoles (227 genera) or *argiotrophy* (93 genera). This suggests that most frog taxonomists have, perhaps in part "inconsciously", followed the "rule" suggested by DUBOIS (1987: 8-9), according to which frog genera containing two or more different developmental pathways (such as *ergotrophy* with free tadpoles, *lecithotrophy* in eggs in shelters, *lecithotrophy* in adult, *adelphotrophy* or *gonetrophy*) should be dismantled either as distinct genera or as subgenera of the same genus. Recent proposals going in this direction (e.g.: DUBOIS, 1987; BOSSLYT & DUBOIS, 2001) have been variously accepted by the community of frog taxonomists, some considering that cladistic relationships are more important than developmental mode as a basis for generic classification. However, it should be stressed that there is no necessary contradiction between the two approaches. Principles of "phylogenetic taxonomy" (e.g.: DE QUEIROZ & GAUTHIER, 1992) or "cladonymy" (DUBOIS, 1997) only require that taxa be holophyletic groups (ASHLOCK, 1971; DUBOIS, 1986), but there is nothing, at least consensually accepted, in cladistic theory to tell us how "high" or "low" in the cladogram should be placed the limit between species-group, subgenus, genus, tribe, etc.

Table 1. Categories proposed for developmental pathways of amphibians, with their major synonyms (terms sometimes found in the batrachological literature for these categories), definitions and examples in amphibians. Rank 2 subcategories are subdivisions of rank 1 categories, and rank 3 infracategories are subdivisions of rank 2 subcategories.

Rank 1 category	Rank 2 subcategory	Rank 3 infracategory	Synonym	Kind and place of pre-imaginal development	Nutritional resources for pre-imaginal development	Examples	
Trogotrophy	Argotrophy	Lecithotrophy	Exotrophy	Free aquatic or terrestrial larva between hatching and metamorphosis	External resources of the aquatic or terrestrial environment	<i>Bufo</i> , <i>Hyla</i> , <i>Rana</i>	
			Endotrophy	Father within a pouch in one of the parents or inside egg capsule in terrestrial or arboreal habitat	No access to the external resources of the environment		
			Endotrophy, lecitrotrophy	Inside or outside egg capsule	Vitelline reserves of the egg		
			Endotrophy: direct development and colous development	Egg deposited in shelter in external environment	Vitelline reserves of the egg	<i>Arthrolepis</i> , <i>Elasmobranchius</i> , <i>Phyllotus</i>	
			Step.lecithotrophy	Endotrophy: ovoviviparity, gastroc-brooding, exoviviparity, paroviviparity	Egg kept in a pouch within or upon one of the parents	Vitelline reserves of the egg	<i>Assa</i> , <i>Nectophrynoides</i> , <i>Rheobatrachus</i>
			Genotrophy	Endotrophy: viviparity, exoviviparity	Free embryo or larva within a pouch in one of the parents	Secretions from a parent	
			Matrotrophy	Endotrophy: viviparity	Free embryo or larva within oviduct of mother	Secretions from the mother	<i>Xenophrynoides</i>
			Patrotrophy	Endotrophy: exoviviparity	Free embryo or larva within a pouch of father	Secretions from the father	<i>Rhinoderma</i>
			Adelpitotrophy	Endotrophy: adelphotrophy	Free embryo or larva within oviduct of mother	Brothers and sisters	<i>Salamandrina atra</i>

Therefore it could well be consensually decided that, as soon as two clades or subclades of frogs display different developmental modes, they should be treated as distinct genera, or at least subgenera (see below). This would have a strong advantage, that of delivering the following clear message to the various categories of non-taxonomists that are users of the nomina of frog species: "whenever two species bear the same generic (or, in some cases, subgeneric) nomen, they have (or are believed to have) the same gross developmental mode". As shown above, there would be very little to change now to homogenize all frog taxonomy in this respect, as this is already "almost" done.

The frequently used formula "developmental mode" should be clarified a little further here. The important point here is to distinguish between different *developmental pathways*. What is suggested here is to take into account, in the taxonomic recognition of supraspecific taxa, the difference between species that follow an ontogenetic trajectory such as that described in the development table of GOSNER (1960), leading to an ergotroph free tadpole, and those that follow an alternative developmental pathway like those reviewed e.g. by THIBAudeau & ALTIG (1999) and evoked above. The important point is here, and not in the place of development of the egg (in an external shelter, or inside a pouch in the adult) or even in the exact developmental stage at which hatching takes place. Thus, it is not suggested here that taxonomic recognition should be given to differences that can be considered "trivial" with respect to the question here addressed, such as the fact that, in some salamander species, hatching can occur either already within the female's genital tract or after deposition of the egg, but with a largely unmodified developmental pathway. In these different populations, at least according to the published data, hatching occurs in different places but there is no evidence that it takes place at different developmental stages or that the development table is modified. Similarly, the term "viviparity", sometimes used (e.g., GARCÍA-PARIS et al., 2003) to designate salamander species that give birth to terrestrial imagos, is misleading. This is just a special case of ovoviviparity, where the embryos start their development with important vitelline reserves, the larvae later may feed by adelphotrophy and development continues very late within the female genital tract, but without exhibiting a particular pathway. In contrast, the term "viviparity" should be restricted to situations where, like in the mammals, the egg does not have important vitelline reserves and the embryos develops thanks to nutrients provided directly by the female in the genital tract. In amphibians, this situation is known only in the bufonid genus *Nimbaphrynoides*.

For the time being, only five anuran genera out of 350 are considered to include both argiotroph species and ergotroph species with free tadpoles (THIBAudeau & ALTIG, 1999): (1) four American genera *Adenomera* Steindachner, 1867 (Leptodactylidae), *Colostethus* Cope, 1866 (Dendrobatidae); *Gastrotheca* Fitzinger, 1843 (Hylidae); *Pipa* Laurenti, 1768 (Pipidae); (2) one Malagasy genus *Mantidactylus* Boulenger, 1895 (Ranidae). In all other regions of the world, all anuran genera are homogeneous regarding their known developmental pathway. Detailed comparisons of developmental pathways between members of both groups are available in some of these cases only (e.g., WASSERSUG & DUELLMAN, 1984), but in the cases where the developmental pathways will prove to be significantly different, it is here again suggested that this should be taxonomically recognized. Nomina are already available to designate the genera or subgenera that would result from dismantlement of the genera *Colostethus* (see DUELLMAN & TRUEB, 1985), *Gastrotheca* (see DUBOIS, 1987), *Mantidactylus* (see GLAW & VENCES, 1994) and *Pipa* (see GORHAM, 1966).

Besides, two anuran genera are known to include two different kinds of lecithotroph development (THIBAudeau & AL FIG, 1999), i.e. both stegolecithotroph and lepolecithotroph. In one case (genus *Eleutherodactylus* Duméril & Bibron, 1841; Leptodactylidae) the eggs may develop either within the mother (*Eleutherodactylus jasperii*) or in an external shelter (all other known species). In the second case (genus *Leiopelma* Fitzinger, 1861; Leiopelmatidae), lecithotroph development may occur within egg (*Leiopelma hochstetteri*) or in a dorsal pouch of the father (*Leiopelma archeyi* and *Leiopelma hamiltoni*). Detailed study of the development of these species are needed to establish whether their developmental pathways are similar, despite the difference of location of the developing egg, or significantly different. In the latter case, it would also be better to recognize subgenera in these taxa, and here also nomina would be available both for *Eleutherodactylus* (see HEDGES, 1989) and *Leiopelma* (see WELLS & WELLINGTON, 1985).

### DEVELOPMENTAL PATHWAYS AND HYBRIDIZATION

Criteria for recognition of taxa can be sorted into criteria for their *delimitation* and criteria for their *rank assignment* in a hierarchical taxonomic system. As well clarified by SIMPSON (1951, 1961), criteria for delimitation of taxa include criteria for *inclusion* and for *exclusion*, and all criteria can be *arbitrary* or *nonarbitrary*. The topology of a cladogram, taken as an accepted hypothesis of relationships between species, can be used as a nonarbitrary criterion for delimitation of taxa, but it provides by itself no criterion for ranking: the cladonomic requirement of holophyly of taxa allows to recognize them but not to allocate them to any category in a hierarchical system. A possible "simplistic" attitude in this respect is to propose the suppression of taxonomic ranks, but the hierarchical structure of taxonomy is critical in allowing the latter to play its rôle of a "convenient information storage and retrieval system" about taxa, their characters, distribution, evolution, relationships, etc. (MAYR, 1981: 511). It should therefore not be suppressed, but made more useful and more general in using nonarbitrary criteria for ranking that allow at least a certain equivalence between taxa of same rank in different groups (see e.g.: DUBOIS, 1988: 66-73, and references therein, AVISE & JOHNS, 1999).

Among other criteria, several authors (VAN GELDER, 1977; DUBOIS, 1981, 1988; PLATEAUX, 1981) supported the use of hybridizability as a nonarbitrary criterion for *inclusion* of different species in the same genus. Interestingly, beside being a criterion for taxa delimitation, this is also a criterion for ranking. On the other hand, DUBOIS (1988) insisted that this criterion should never be used for *exclusion*. In other words, according to this criterion, the fact that two species are able to give birth to viable true diploid adult hybrids is to be used as evidence that these two species belong in the same genus, whereas the absence of hybridizability provides by itself no useful information for the generic allocation of two species. It is important to stress here that hybridizability of species, as strictly defined by DUBOIS (1988), is a taxonomic criterion but not a phylogenetic criterion, as there is no direct correspondence between hybridizability and cladistic relationships: hybridizable species are not necessarily cladistically sister-species, but may be quite distantly related (see e.g. the case of European green frogs of the subgenus *Pelophryllax* GÜNTHER, 1990: 258). Reasons for this are easy to understand, as this is linked to the necessity for closely related species to develop isolation mechanisms in

sympatry or parapatry, but not in allopatry (see DUBOIS, 1988). Hybridizability (or its absence) between two species is not a "character" of any of these species, and is therefore neither plesiomorph nor apomorph: if it were so, each species would have millions of characters, according to its potential hybridizability with all other living species. It is rather a "relational taxonomic criterion" (DUBOIS, 1988), or more shortly a *relacter* (from the Latin *relatio*, in the sense of "relation between two things", and *character*, in the sense of "character, mark that distinguishes something"). Relacters are of various kinds, as discussed in detail by DUBOIS (1988). e.g., sympatry-parapatry-allopatry, parasitic specificity, ecological competitive exclusion, presence-absence of a hybrid zone and of a gene flow between two parapatric entities, etc. Using such a relacter as hybridizability to build up taxonomies is a way to acknowledge that taxonomy does not rely only on characters and relationships, but on other kinds of information. Similarly, the absence of gene flow in the field between two parapatric entities is a way to establish the specific status of these two entities, although the two kinds of information on which this decision is taken (parapatric geographic distribution and absence of gene flow) do not pertain to any of the two entities taken by itself, but characterizes their *relation*.

Just like the criterion of similar developmental pathway discussed above, the principle of hybridizability as a nonarbitrary criterion for inclusion in a genus can perfectly be used within the frame of a system of phylogenetic taxonomy: one just has to place the "bar" of the genus rank just at the level of hybridizable species pairs, and use consistently the principles of cladonomy for all other taxa. Advantages of this system upon any other arbitrary or "consensual" delimitation of genera were discussed at length elsewhere (DUBOIS, 1988). The new question that may be asked here is: what can be the relationships between this criterion of hybridizability and the criterion of similar developmental mode?

Although a number of artificial hybridizations have been carried out in the past in amphibians (reviews in MONTALENTI, 1938, MOORE, 1955, BLAIR, 1972), none of these reported experiments involved argiotroph, particularly lecithotroph, anuran species, either between themselves or with species of the same groups having free tadpoles. A rapid a priori thinking might suggest that there is no need to try such crossings, because of course the "developmental program" of a species with tadpole is unlikely to be compatible with that of a lecithotroph species, and such a combination appears bound to fail at a rather early stage of development. However, until the experience is carried out in different anuran groups including both kinds of species, this possibility cannot be theoretically ruled out. In amphibians, hybridization can at least partially succeed between species with rather different developments (e.g., MARTÍNEZ RICA et al., 1984), and in fishes it can be successful, at least up to a certain point, between species that are considered only distantly related (e.g., WHITE et al., 1973).

Particularly interesting in this respect are the works on the frog genus *Gastrotheca* by several authors (DEL PINO, 1980, SCANLAN et al., 1980, DEL PINO & ESCOBAR, 1981, WASSER-SUG & DUFFELMAN, 1984) which suggest that in this genus lecithotroph development was plesiomorphic, but that, in several distinct groups of high altitude populations, a reversal to a development through a free tadpole stage occurred. Under such a scenario, rather than a *replacement* of a developmental program by another, what would have occurred is the



appearance, possibly through phenomena of *duplication of regulatory genes* (GOULD, 1977; RAFF & KAUFMAN, 1983), of a new developmental program *beside* the initial one, which would be conserved in the genome, but unused, "in dormancy", in some species. The possibility of a "switch" from one program to another, on the occasion of speciation events, would allow these frogs to adapt to new ecological conditions or to conquer new habitats. Such a scenario may have developed in several groups of frogs including both ergotroph with tadpoles and lecithotroph species, and indeed the possibility of its occurrence in the genus *Philautus* is suggested by the topology of the cladogram published by MEEGASKUMBURA et al (2002a): if this cladogram was confirmed (but see DUBOIS, 2004a), lecithotrophy would have appeared independently twice, in two groups of species (the Indonesian-Indochinese, and the Indian-Sri Lankan, ones) nested within a clade of ergotroph rhacophorids.

If two different developmental programs can indeed be conserved in parallel in the genome of some species, then this would open the possibility of successful hybridization between species having different developmental pathways: in the early hybrid embryo, the regulatory genes of one of both species might "take over" those of the other one, and "impose" the use of one developmental pathway. At this stage, this suggestion is purely theoretical, but experimental testing of this possibility, between closely related species having different developmental modes, might be very rewarding. Given the difficulty to carry out such hybridization experiments in all rigour (with control crosses, caryological and electrophoretic assessment of the real hybrid, and not gynogenetic, nature of the embryos, etc ; see DUBOIS, 1988), such experiments would certainly have more chances to be successful if carried out with fresh animals just collected in the field, i.e. close to their natural populations in their native countries.

Should hybridization prove successful, in some cases, between ergotroph and argiotroph species, this would require, in order to follow both the hybridizability criterion (DUBOIS, 1988) and the criterion of similar developmental mode (DUBOIS, 1987), to place these species in different subgenera of the same genus. If reversion from one developmental mode to another occurred independently in several different groups, these groups should be treated as different subgenera of the same genus, as suggested by DUBOIS (1987) in the genus *Gastrotheca*. On the other hand, in other cases, e.g. in groups where lecithotroph species are not known to have closely related species, it may be unlikely to ever find ergotroph species that would have retained the ability to hybridize successfully with them. In such cases, if there is no conflict with the other criteria suggested (DUBOIS, 1988: 76-77, 105-108), the two groups should be recognized as distinct genera, not subgenera.

#### DETAILED PROPOSALS REGARDING GENERIC TAXONOMY

In zoology, the establishment of supraspecific taxa and of their taxonomic ranks, under the guidelines suggested above, can rely upon several nonarbitrary criteria. In frogs, among other criteria, three powerful ones are holophyly of taxa (delimitation criterion), common development pathways of species (delimitation criterion) and hybridizability between species (both delimitation and ranking criterion). To make clearer the hierarchical relationships between these criteria, the hypothetical cladograms presented in fig. 1 can be commented in

some details. All these cladograms, involving six species, have the same topology, but include different kinds of information regarding developmental pathways and hybridization. As will be shown in detail below, in some cases the use of the criteria presented above lead to clear and unique proposals regarding taxa that should be recognized as genera or subgenera, whereas in other cases these criteria alone are not enough to decide among several possibilities: in these latter cases, other criteria must be used to go further, as discussed e.g. by MAYR (1969) or DUBOIS (1988), but these further steps won't be considered here.

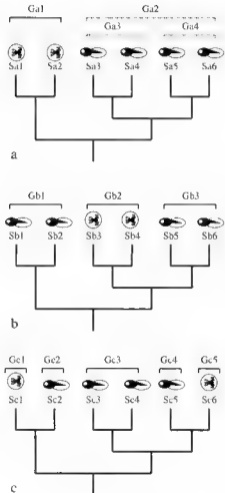
In the three cladograms of figures 1a-c, no information is available regarding hybridization, but some species are known to develop through a free aquatic tadpole stage, whereas others have leipolecathotroph development, e.g. direct development in eggs deposited in terrestrial shelters. According to the proposals above, genus rank should be afforded to groups of species that share a developmental pathway. In order to respect the principles of cladonomy, i.e. to recognize only holophyletic groups as taxa, this results in a different number of genera according to the distribution of developmental pathways among the six species. Note that in the situation of figure 1a, the use of this criterion alone does not allow to decide whether a single genus, or a genus with two subgenera, or two distinct genera, should be recognized among the four species with tadpoles, but in the two other cases no such uncertainty exists.

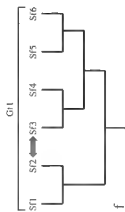
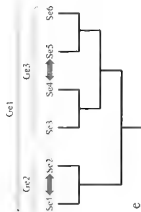
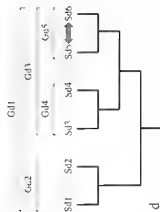
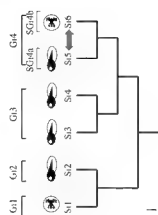
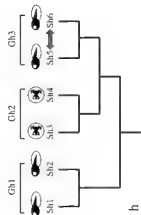
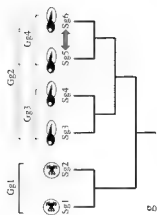
In the three cladograms of figures 1d-f, no information is available regarding developmental pathways, but data are available about some pairs of species that are known to be liable to give birth to viable true diploid adult hybrids. Here also, in some cases the information provided by hybridizability does not allow to choose between several generic taxonomies, as hybridizability is only a criterion for inclusion (i.e. for grouping species in a single genus) but should never be used for exclusion (i.e. for splitting genera). However, in some cases, like that shown in figure 1f, information on hybridizability of two quite distantly related species may be enough to stabilize the generic taxonomy of a whole group.

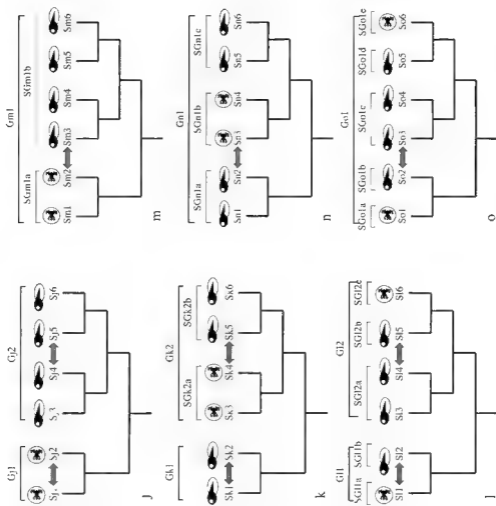
Now, let us consider the consequences of combining information on developmental pathways and information on hybridizability in a single cladogram. Crossing the three situations of figures 1a-c with the three situations of figures 1d-f gives nine different situations, presented in figures 1g-o. Taxonomic decisions in these nine situations must follow a hierarchy between criteria, as proposed in detail by DUBOIS (1988: 82-84): according to this hierarchy, data on hybridizability must be used first, to establish which species cannot be placed in different genera. This means that, in the hypothetical case (not yet known to be indeed possible in some groups of amphibians) where species showing different developmental pathways would be able to give viable true diploid adult hybrids, they should be placed in the same genus: but then they should be referred to different subgenera. Such hypothetical situations are shown in figures 1i, 1k, 1l, 1m and 1n. After the criterion of hybridizability, developmental data should be used to split further some genera into subgenera (in the exceptional case just mentioned), or, more frequently, to decide between alternative generic taxonomies among which the hybridization criterion alone does not allow to choose. Thus, in the situation of figure 1d, hybridization data do not allow to choose between recognizing one, two or three genera. In figure 1g, developmental data allow to recognize a distinct genus for the species Sg1 and Sg2, but still do not allow to decide between one or two genera for the species Sg3 to Sg6, this decision will have to rely on other pieces of information. In contrast,

Fig. 1. - Cladograms showing hypothetical relationships between six frog species and providing information on their developmental pathways and hybridization between them. Abbreviations of taxa include a capital letter for rank of taxon (S, species; SG, subgenus; G, genus), a different lower-case letter for each subfigure (a, b, c), a number for each species or genus, sometimes followed by a letter for subgenera within a genus, thus SG.4a is the first of the two subgenera of genus 4 in figure 1. The symbol 1 indicates species with free aquatic ergotroph tadpoles and the symbol 2 indicates species with leipolecithotroph development (direct development in eggs deposited in terrestrial shelters). Species liable to give birth to viable true diploid adult hybrids are connected by the symbol 3. Generic and subgeneric taxa recognized on the basis of the information provided are shown at the top of figures as square brackets that can be continuous line (in the case of nonambiguous taxonomies, symbol 4 for genus, symbol 6 for subgenus) or composed of hyphens (in the case of several possible alternative taxonomies, symbol 5 for genus). (a-c) Only information on developmental pathways is available, but none on hybridization. (d-f) Only information on hybridization is available, but none on developmental pathways. (g-o) All possible combinations of cases (a-c) and (d-f) with both kinds of information available.

Symbols







in figures 1h and 1i, the combined use of the two criteria here proposed allows to decide without ambiguity which groups should be recognized as genera, and which as subgenera.

As discussed already in DUBOIS (1988), supraspecific taxa defined under such guidelines are likely to be more informative than taxa just recognized by simple "consensus" but without any clear theoretical background. After a brief period of change, the new taxonomy may prove more useful both for taxonomists and non-taxonomists and for various kinds of studies and comparisons. As information on hybridizability and developmental pathways, once obtained, is not liable to change (in contrast with the topology of cladograms), a generic taxonomy using these criteria would be more stable in the long run than a generic taxonomy based on cladistic hypotheses alone, but ignoring these biological criteria.

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